A NEW ENCHODONTID FISH GENUS FROM THE UPPER CENOMANIAN OF JERUSALEM, ISRAEL

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ABSTRACT. *Parenchodus longipterygius* n. g. et sp. belonging to the Enchodontidae is described on the basis of eight specimens. These were found in platy limestones of the late Cenomanian Kefar Shaul Formation, in the vicinity of Jerusalem, Israel. The species is characterized by a short, high body, a fenestra-less premaxilla, and by the long and narrow postcleithrum reaching the ventral margin of the belly. Other characteristics are the axial skeleton with thirty vertebrae, of which only seven are abdominal; dorsal and anal fins with long bases; a ventral, well-developed pectoral fin; a naked body, devoid of scales except for two dorsal postoccipital and three lateral scutes at the base of the tail; and with a reduction and fusion of the endoskeletal elements of the caudal fin. The fish was a small, fast swimming predator. The structure of the head, the absence of scales, and the fusion of the caudal fin elements suggest that this genus is related to *Enchodus*.

FINDS of fossil fish in the vicinity of Jerusalem have been recorded since the beginning of the century (Blanckenhorn 1905; Shalem 1925, 1927), however, they have never been studied in detail. The fossil fish come from the Laminated Limestone Member, which constitutes the upper part of the Kefar Shaul Formation and overlies its Lower Argillaceous Member.

The Laminated Limestone Member consists of buff to yellowish-white, red stained, thin-bedded, laminated to platy (up to 15 cm), fine-grained limestone with argillaceous material between the plates (Arkin *et al.* 1965, p. 20; Braun 1970, p. 33). The formation is overlain by the dolomitic, partly calcareous Weradim Formation, and overlies the dolomitic-calcareous Amminadav Formation. The complex of strata belongs to the Judea Group which is widely extended in Israel.

The distribution of the fish-bearing Laminated Limestone Member around the type locality is very restricted. It extends over less than 10 sq. km, in varying thicknesses up to 15 m, and is confined to the eastern flanks of the Judea anticline, in the western outskirts of Jerusalem.

Another restricted occurrence of fish-bearing strata, of a similar lithology and more or less in a similar stratigraphic position, is exposed near the town Ramallah, some 20 km north of Jerusalem.

The underlying Argillaceous Member is thicker, up to 60 m thick, and though of greater extent than the Laminated Limestone Member, it wedges out in all directions, within a distance of up to a few tens of kilometres.

The overlying Weradim Formation is much more extended than the Kefar Shaul Formation. Its thickness ranges from 25 to 115 m, and where the Kefar Shaul Formation is missing, it directly overlies the Amminadav Formation (Braun 1970). These field relationships may be an indication that the Weradim Formation gradually replaced the Kefar Shaul Formation.

The fish-bearing Laminated Limestone Member is quite poor in fossils of other groups. The fish assemblage comprises several holosteans, and many teleosts, which have not yet been studied. Some pelecypods, echinoids, and especially ammonites, though badly preserved, enable dating the member as of late Cenomanian age (Shalem 1925, 1927; Picard 1938). The fishes are also accompanied by crustacean and terrestrial plant remains (Lewy and Raab 1976).

Thin sections examined microscopically revealed finely laminated micrites, rich in faecal pellets, filamentous algae, and fish teeth and scales. Rare planktonic and benthonic foraminiferids also occur (Hamaoui and Raab, 1965 pp. 34–35).

A low energy, marine environment of restricted, shallow, partly closed basins was suggested (Lewy and Raab 1976, p. 32.5).

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The underlying Argillaceous Limestone Member of the Kefar Shaul Formation is very rich in invertebrate megafossils. Assemblages comprising pelecypods, echinoids, and especially ammonites (e.g. *Turrilites costatus* Passy and *Neolobites vibrayeanus* (d'Orbigny)) assign a late Cenomanian age to the member (Avnimelech and Shoresh 1962; Lewy and Raab 1976).

The overlying Weradim Formation, which partly replaces the Kefar Shaul Formation (see above), is poor in fossils, most probably due to extensive dolomitization. However, in places, especially in quartzolitic lenses, various pelecypods, particularly rudists (known as reef builders) were recorded (Braun 1970, p. 33; Shalem 1927: 'calcari superiori a Radioliti').

METHODS AND TECHNIQUES

The exposed side of the specimens, which were embedded in fine-grained limestone slabs, was mechanically cleaned under a stereoscopic binocular, with the aid of needles and fine brushes. The slabs were then embedded in polyester resin and later soaked in 10% acetic acid to remove the enclosing calcareous matrix of the underside (Rixon 1976).

SYSTEMATIC PALAEONTOLOGY

Suborder ENCHODONTOIDEI Berg, 1940
Family ENCHODONTIDAE Lydekker, 1889

Diagnosis. (Emended, after Goody 1969, p. 71.) Head deepened, especially posteriorly; body may be deepened in thoracic region. Posttemporal fossa unroofed. Lower jaw long and deep behind the constricted symphysis; articular facet visible in lateral view. Opercular convex posteriorly, and deeper than it is broad; preopercular without prominent ventral spine. Pectoral fins larger than pelvic fins and extremely low on body. Pelvic fins abdominal. No posterior extension of the cleithrum. Lateral line scales present or absent, if present they do not overlap; mid-dorsal scutes reduced and not overlapping.

Genus PARENCHODUS n.g.

Diagnosis. A fish with a short, high, and laterally compressed body. The length of the head exceeds one third of the standard length, slightly exceeding also the depth of the head at the occipital region. The maximal depth of the body is half the standard length. The obit is large, its length reaching one third of the length of the head. The premaxilla lacks a fenestra for reception of the end of the large dentary tooth. Postcleithrum well developed, long and narrow, reaching the ventral margin of the belly. Axial skeleton with thirty vertebrae, twenty-three of them caudal. Dorsal fin with a long base, occupying most of the back, reaching the caudal peduncle.

Body naked, except for two unequal, not overlapping scutes on the mid-dorsal, postoccipital region, and three overlapping lateral scutes on each side of the caudal peduncle. The bases of the caudal fin rays deeply embrace the hypural plates.

Etymology. Para (Greek), near—resemblance to *Enchodus.*

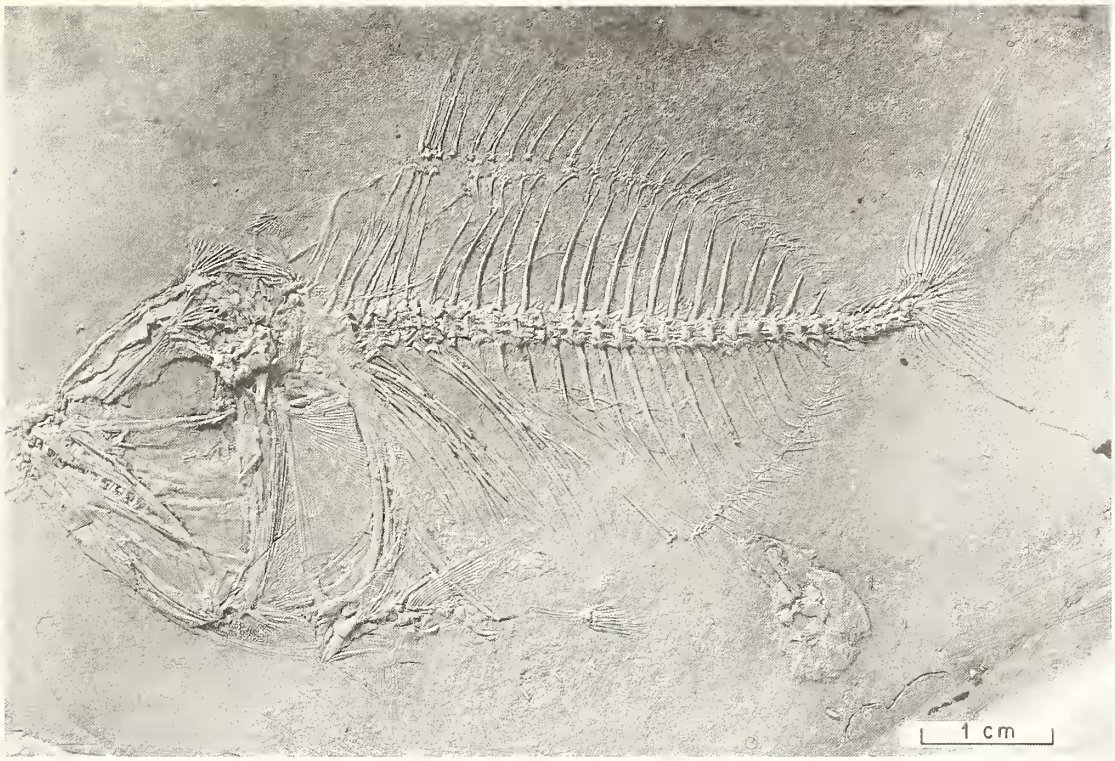
Type species. Parenchodus longipterygius n. sp.

Parenchodus longipterygius n. sp.

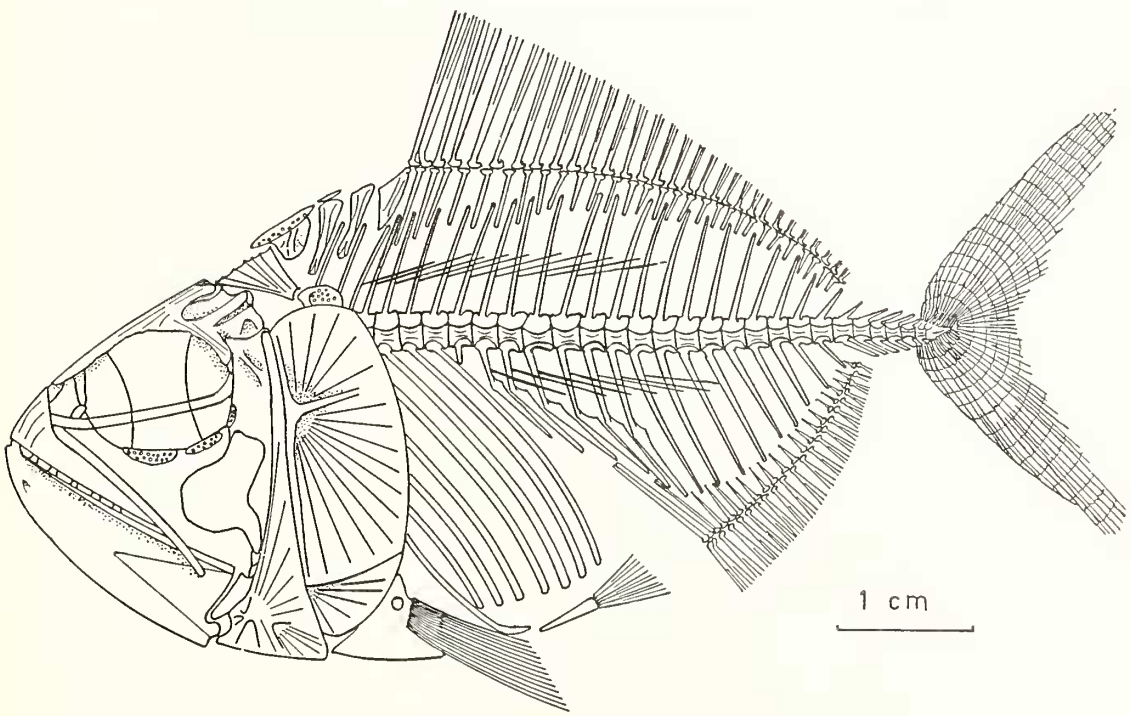
Diagnosis. Parenchodus of up to 75 mm standard length, with fin rays counting as follows: dorsal fin, 30; pectoral fin, 14; pelvic fin, 5; and anal fin, 22.

Holotype. P.163, The Hebrew University of Jerusalem. An almost complete fish embedded in resin (text-figs. 1 and 2).

Referred material. Seven specimens: P.143, P.150, P.1502, P.1503 (text-fig. 3), P. 1504, P.1508 (text-fig. 7), HUJ. DY-15, deposited in The Hebrew University of Jerusalem.



TEXT-FIG. 1. *Parenchodus longipterygius* n. g. et sp. Holotype, P.163, Upper Cenomanian, Kefar Shaul Formation, Jerusalem, Israel. An almost complete specimen. Left side.



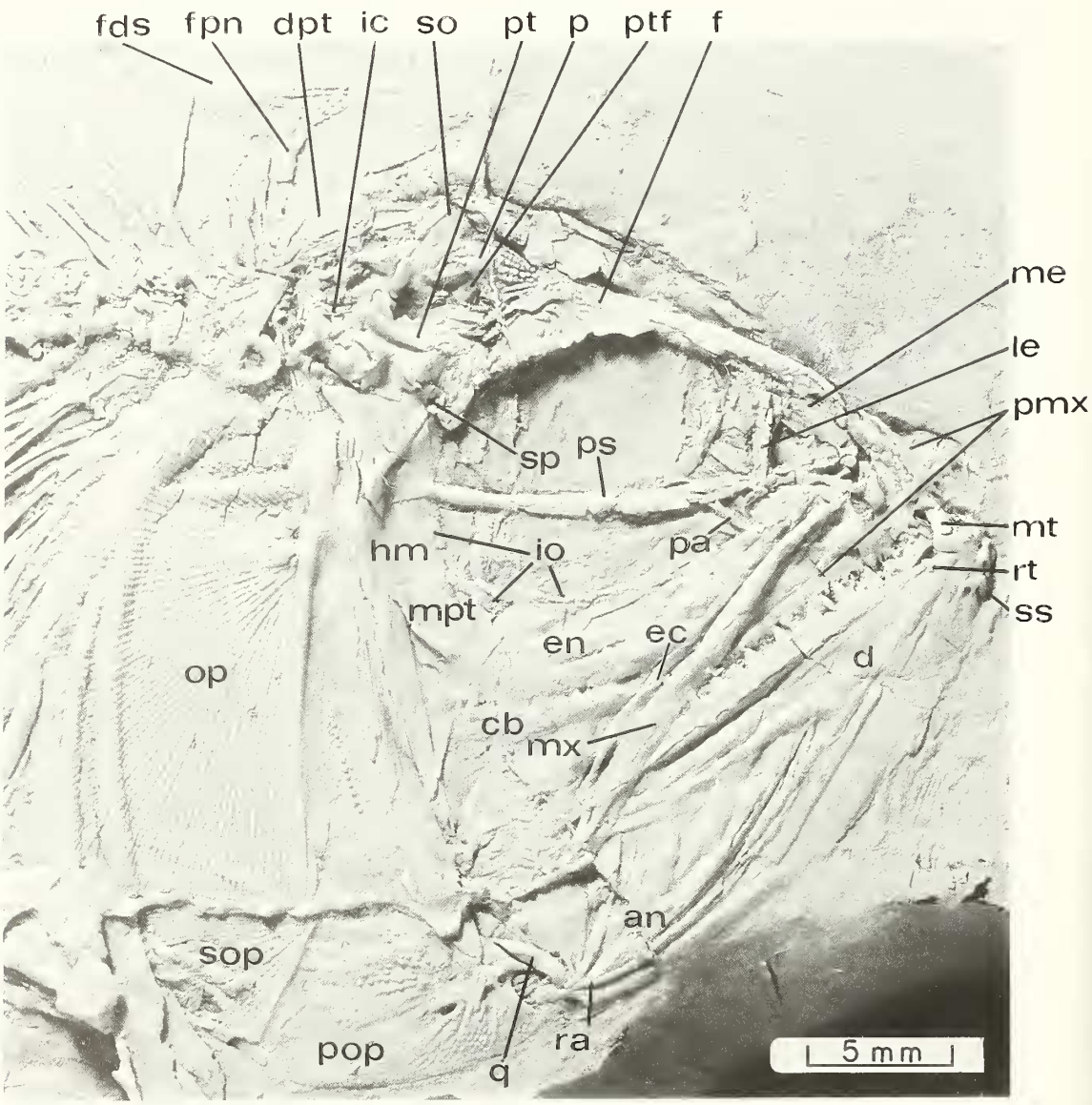
TEXT-FIG. 2. *Parenchodus longipterygius* n. g. et sp. Restoration of the skeleton, lateral view.

Locality and horizon. Givat-Shaul, a western suburb of Jerusalem. The Upper Cenomanian, laminated limestone Member of the Kefar-Shaul Formation.

Etymology. Longipterygius—having a long fin.

DESCRIPTION

General features. The body is short, deep, and laterally compressed. Its maximal standard length is 75 mm, slightly more than twice its maximum depth. The head is short and deep; its length slightly



TEXT-FIG. 3. *Parenchodus longipterygius* n. g. et sp. P.1503, Upper Cenomanian, Kefar Shaul Formation, Jerusalem, Israel. Lateral view of the skull.

TABLE 1. Dimensions (in mm) and ratios of six specimens of *Parenchodus longipterygius* n. g. et sp.

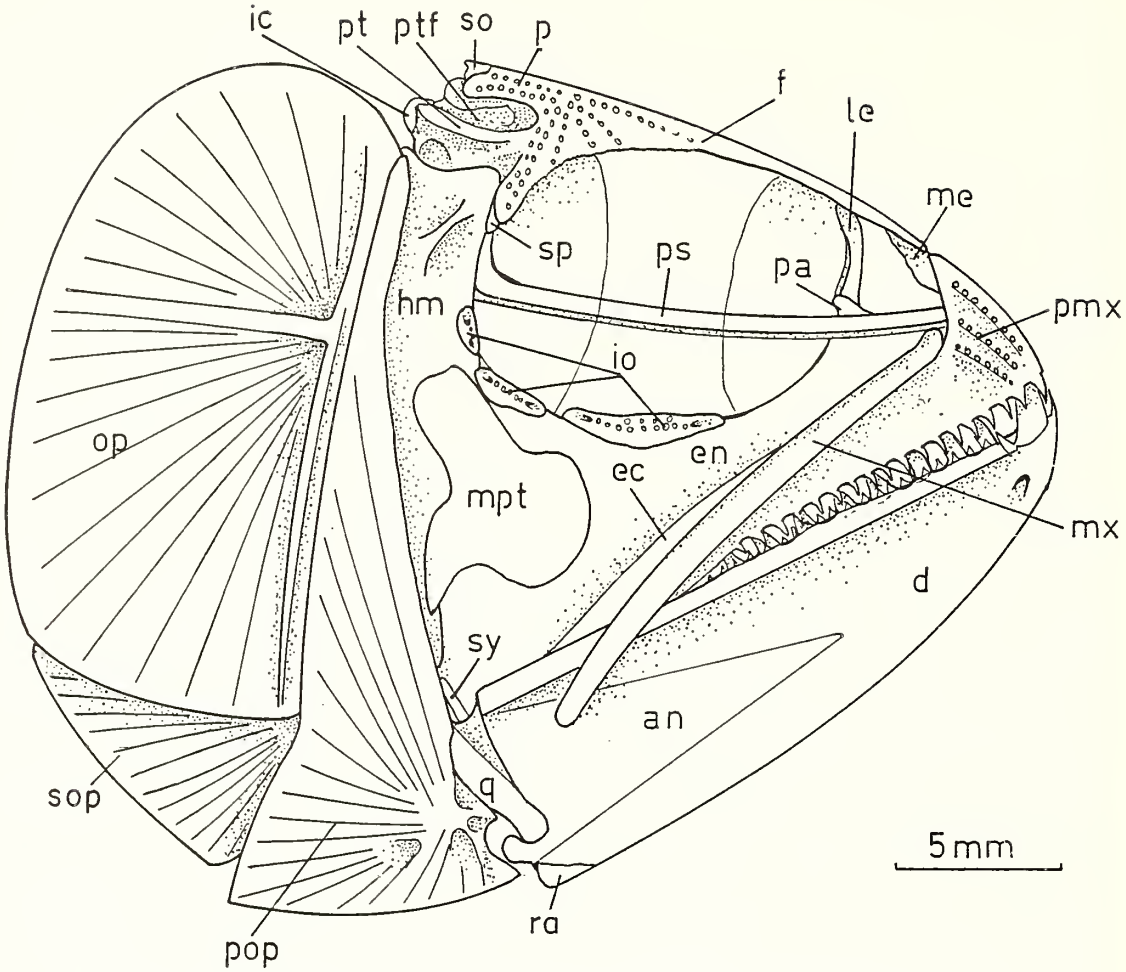
Specimen	P.1502	P.163	P.143	HUJ. DY-15	P.1503	P.1504	Mean
Standard length	61	67	69	74·5			
Maximum depth of trunk	23	35	34	31	34		
Depth of trunk as percentage of standard length	37	52	49	41			44
Length of head	23·5	29	31	29	31	28	
Length of head as percentage of standard length	38	43	44	38			40·75
Depth of head	23	25	28·5	25	27·5	24·5	
Depth of head as percentage of head length	97	86	91	86	88	87	89
Length of orbit		8	8	11·5	9·5	9	
Length of orbit as percentage of the head length		28	26	40	31	32	31·4

exceeds its maximal depth at the occipital region, and is more than one third of the standard length. The oral gape is wide, the length of the lower jaw is about three times its maximum depth. The orbit is large, occupying half the length of the neurocranium. The dimensions of 6 specimens are given in Table 1. The post- and preorbital regions are narrow. Three infraorbitals exist. The postcleithrum is narrow and long, reaching the ventral margin of the belly. There are 30 vertebrae of which 23 are caudal. The dorsal fin is long and consists of 30 fin rays. The pectoral fin is in a ventral position and consists of 14 fin rays. The pelvic fin is smaller than the pectoral fin, in abdominal position, and consists of 5 fin rays. The anal fin has a long base and consists of 22 fin rays. The caudal fin is deep, deeply forked with a very narrow peduncle, carrying flat neural and haemal spines, strongly inclined backwards. The anterior haemal spines have a wide and shallow proximal part. Three supraneurals exist. Dentition well developed. The palatine carries one large, striated conical tooth. The ectopterygoid bears large teeth. The dentary has 2 rows of conical teeth. The typical anterior mandibular tooth is exceptionally large—about a quarter of the total length of the entire lower jaw and longer than the palatine tooth. The maxilla is toothless. One row of narrower and high conical gill-rakers exists on the floor of the anterior part of the gill chamber.

The body is naked, except for two large, not overlapping, unequal scutes, at the mid-predorsal. Three lateral scutes exist at the base of the caudal fin; they are large, overlapping and have crenulated margins.

Neurocranium and the skull roof (text-figs. 3 and 4). The skull roof is flat, anteriorly narrow becoming wider posteriorly, widest above the posterior part of the orbit. Its posterior margin is notched by a wide, unroofed posttemporal fossa. The neurocranium is deep and wide posteriorly, becoming narrower anteriorly. The orbit is large, occupying more than half the length of the neurocranium. The posterior margin of the skull roof extends backwards laterally.

The frontals form most of the skull roof, meeting along the median line in a sinuous suture. At the posterodorsal corner of the orbit, the frontal widens abruptly laterally, forming a wing-like process, inclined ventrally in front of the sphenotic. This process builds the front wall of the posttemporal fossa (text-figs. 3 and 4). The frontals reach the premaxillae anteriorly. Their surface is ornamented by prominent ridges, radiating from the centre of ossification, which is situated above the posterior part of the orbit. The ridges in front of and behind the centre of ossification are tuberculated, whereas laterally they are replaced by closely spaced tubercles. The lateral margins of the frontals are crenulated. A branching point of the supraorbital sensory canal occurs in front and close to the centre of ossification of the frontals. One branch is directed anteriorly along the bone; a second runs



TEXT-FIG. 4. *Parenchodus longipterygius* n. g. et sp. Restoration of the skull. Lateral view.

posterolaterally along the lateral expansion to the pterotic, and a third turns backward, mesial to the posttemporal fossa, passing to the parietal.

The parietals are small and narrow, in close contact with the posterior margin of the frontals. They are located mesial to the posttemporal fossae. The dorsal surface of the bone is tuberculated.

The supraoccipital is small, median, separating the parietals. A low crest extends along the median line of the supraoccipital from the anterior to the posterior end, without protruding posteriorly. The surface of the bone is smooth.

The sphenotic is situated at the posterodorsal corner of the orbit, posteroventral to the wing-like lateral process of the frontal. The lateral surface of the sphenotic is triangular and slightly tuberculated. The exposed part of the pterotic is very thick, forming the posterior continuation of the lateral process of the frontal. A ridge runs along the middle of the bone, bordering the posterolateral side of the posttemporal fossa. The dilatator fossa lies lateral to the ridge.

The parasphenoid is beam-like in lateral view, with a low ventral carina along it. Beyond the orbit the carina expands ventrally and the beam dorsally to meet the prootic. The parasphenoid terminates anteriorly in front of the anterior end of the maxilla.

The features of the prootic, including the arrangement of its foramina, generally fits the enchodontid prootic, as described by Goody (1969, p. 85, fig. 38B).

The mesethmoid is well developed and ossified. Its dorsal side is covered posteriorly by the frontal and anteriorly by the premaxilla.

The lateral ethmoid is a beam-like bone. Its ventral face is grooved to accommodate the dorsal process of the palatine.

The circumorbital bones are represented by only three thin infraorbital plates, which housed the infraorbital sensory canal. They extend from the centre of the posterior margin of the orbit to the centre of its ventral margin, without touching each other. The anterior one is the longest and the posterior one is the shortest.

The intercalar is the only bone that could be identified in the posterior wall of the neurocranium, as a well-developed thickening below the pterotic.

An incomplete interorbital septum forms two wings, penetrating into the anterior and posterior regions of the orbit, but not meeting.

Hyopalatine bones (text-figs. 3 and 4). The hyomandibular is narrow and long, forwardly inclined. The upper half of the bone is flat, carrying a prominent arched ridge, running obliquely from anterodorsal to posteroventral. It is wide, plate-like, with a thick, wedge-like lower part.

The symplectic is small and wedge-like with about half its length inserted in the groove of the quadrate.

The quadrate is a narrow, high triangle. The ventral apex of the triangle is rounded, slightly arched posteriorly. The bone is relatively thick and its surface is striated, except for its anterior and dorsal margins, which are thin and smooth. A deep groove exists in the upper part of the inner side of the bone, for the symplectic.

When the mouth was closed the lower jaw covered the anterior margin of the quadrate and only its thickened part remained exposed in lateral view.

The endopterygoid is thin and large, forming most of the infraorbital region. It carries tubercle-like teeth. Its posterodorsal part is covered by the metapterygoid.

The dorsal margins of the ectopterygoid are exposed dorsal to the maxilla. The ectopterygoid continues forward, covered by the maxilla and the premaxilla. It is long and flat, and bears along its entire margin a row of high conical teeth (similar to the premaxillary teeth).

The metapterygoid is thin with rounded margins, except for the posterior ones which extend into two lobes, a dorsal one, prominently ridged and a ventral one, thin and flat. Both lobes overlap the hyomandibular, below its mid-length.

The palatine is thick and short and bears posteriorly a dorsal process which fits a groove in the ventral side of the lateral ethmoid. In lateral view the palatine is recognized as a thickening behind the premaxilla. It bears at its anterior end a very large, somewhat compressed, striated tooth.

Upper jaw. The premaxilla is triangular, with a posteriorly extended base. The frontal area of the premaxilla is tuberculated and its lateral area is smooth. The premaxilla forms more than three-quarters of the margin of the upper jaw and bears thin, high conical teeth, similar in size to the smaller teeth of the lower jaw (see below p. 724). The foremost tooth is the largest, the others becoming gradually smaller backwards. The fenestra in the premaxilla, so typical of enchodontids (Goody 1969, p. 71) was not observed.

The maxilla is long, rod-like, thick anteriorly, wide and flat posteriorly, toothless. Its anterior part is situated along the dorsal margin of the premaxilla, crossing the gape at an angle of about 45°. The anterior end of the maxilla is slightly bent ventrally, and is situated below the premaxilla, probably in a groove in its inner side. The surface of the maxilla is smooth.

Lower jaw. The lower jaw is relatively high, especially in its posterior part; its maximum height is about one third of its total length (text-fig. 3).

The angulo-articular is well developed, triangular, with ventral margin extending forward almost to the mid-length of the jaw. It is ornamented by strong tuberculated ridges, radiating sparsely from a

centre near the articulation of the jaw. It bears a postarticular process, which fits in a notch at the ventroanterior end of the preopercular. The retroarticular is reduced to a small bone situated in the posteroventral corner of the lower jaw.

The dentary is smooth, except for a fine radial striation originating from a centre near the symphysis. The dorsal margin of the dentary thickens into a wide flange, reaching the symphyseal region, and bearing two rows of teeth. The external row contains numerous, closely spaced, high, conical, smooth, sharp teeth, which are somewhat irregular in size, though the anterior ones are larger. A second, internal row, consists of seven to eight high, thick, slightly laterally compressed and striated teeth. The size of these teeth is almost twice that of those of the outer row. The foremost tooth of the inner row is the largest. This large tooth (text-figs. 3 and 5A)—so typical for the genus *Enchodus*—protrudes just beyond the symphysis. It is very high, its height slightly exceeding a quarter of the length of the jaw. Its base is wide and its surface smooth. It is situated on the margin of the jaw, with a slight forward inclination. The tooth has an asymmetric cross-section, with a convex posterior face, and a flat to concave anterior face. It has two cutting edges, one anterolateral and the other posteromedial. A smaller tooth could be observed laterally and behind the foremost fang in specimen P.163. A smaller tooth (relatively to the fang) and in a similar position and direction is illustrated by Woodward (1903, pl. 14, fig. 7). Such teeth, so close to the fangs, do not seem functional and hence might be regarded as replacement teeth. The symphyseal region is relatively high, and its dorsal margin lipless. The symphysis is built of three interlocking finger-like processes on each dentary. A conspicuous foramen of the mandibular sensory canal is situated just behind the symphysis.

Branchial arches and branchiostegal rays. The ceratohyal and the hypohyal (seen on the right side of specimen P.143) constitute one beam-like element, extending backwards from the middle of the lower jaw to the posterior end of the preopercular.

The beam bears eleven posteriorly arched branchiostegal rays. These are long, thin, and have a thickened base. A pair of high and thin beam-like first ceratobranchials (text-fig. 3) carry high, slender, slightly anteriorly inclined gill-rakers.

Operculum. The opercular bones form together a narrow cover, twice as high as its maximum width.

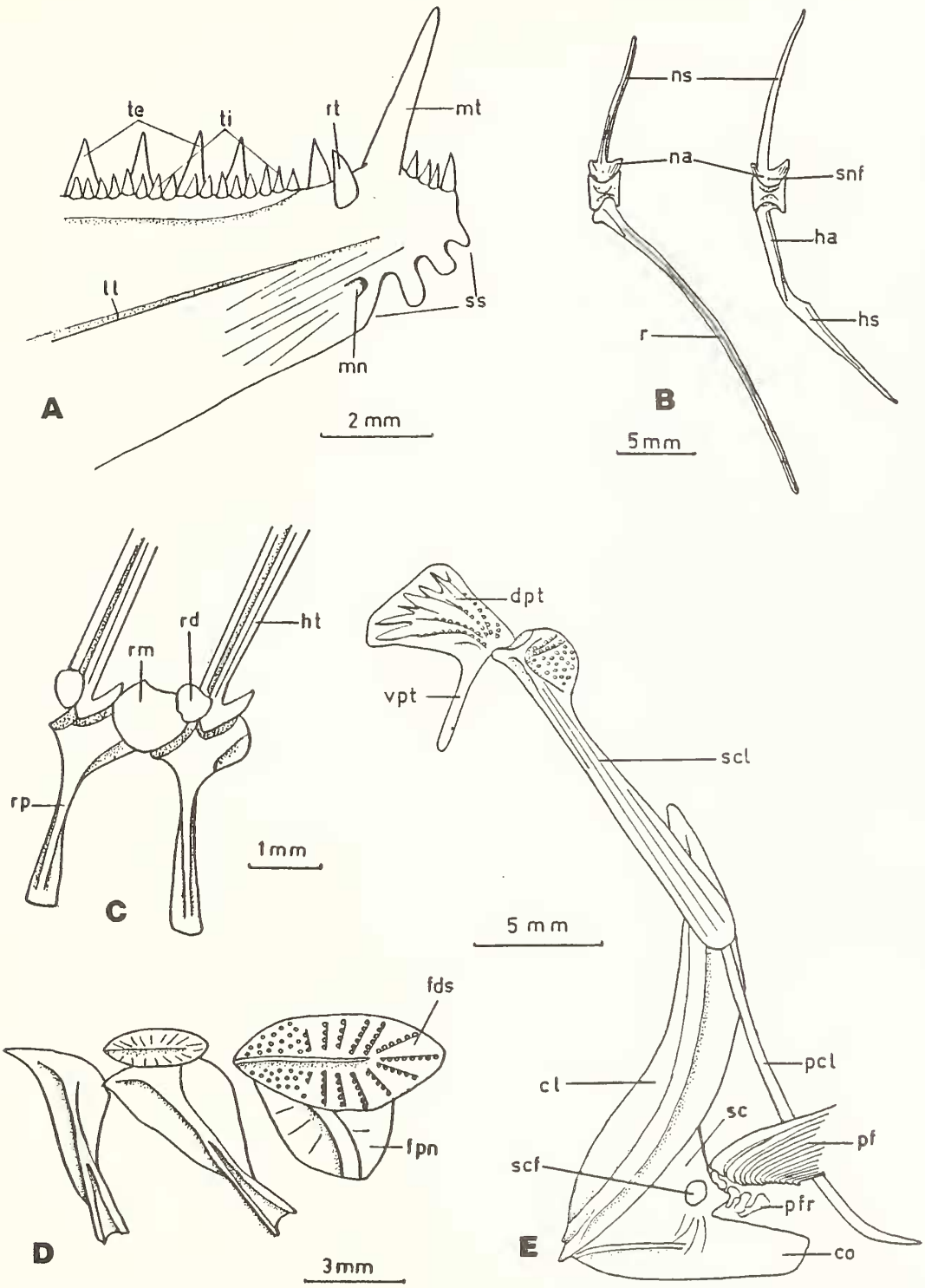
The opercular is narrow and high. Its dorsal, posterior, and ventral margins form a continuous arched line. The anterior margins are almost straight, perpendicular to the body axis. Its articular condyle with the hyomandibular is located at about two-thirds of its height. An inner, supporting beam extends from the condyle backwards, and another along the anterior margins, just beyond the area covered by the preopercular. The surface of the opercular is covered by finely tuberculated prominent ridges, radiating from the centre of ossification, which is situated near the condyle.

The triangular subopercular is slightly overlapping the ventral margins of the opercular. It is ornamented by finely tuberculated ridges, radiating from the anterodorsal corner.

The preopercular is thick, high-triangular, with a posteriorly and anteriorly extended ventral base. In its anteroventral corner there is a socket for the postarticular process of the lower jaw. Tuberculated ridges radiate from a centre beyond the articulation socket, changing dorsally, and especially along the anterior margin, into fine striae. The preopercular sensory canal ran along the preopercular, opening through three large pores in the anteroventral area of the bone. From the anteriormost opening, which is directed forward, the lateral line canal continued to the mandible. Interopercular bone absent.

Axial skeleton. The vertebral column numbers 30 vertebrae, of which only 7 are abdominal and 23 caudal. Eadh centrum is almost quadrangular and strongly constricted in the middle. A finely striated ridge runs along the lateral side of each centrum. The centra are approximately equal in length along most of the body, however an abrupt shortening occurs at the caudal peduncle. A high neural arch extends all along each centrum, not fused with it (text-fig. 5B). The neural arch comprises a narrow prezygapophysis, and a high and wide postzygapophysis, both with a delicately striated surface. The centre of the lateral side of each neural arch is pierced by the foramen for the spinal nerve.

In the abdominal region the neural spines are paired. They originate at the anterior part of the



TEXT-FIG. 5. *Parenchodus longipterygius* n. g. et sp. Restoration of: A, anterior part of right lower jaw. B, abdominal vertebra no. 7 (*left*) and precaudal vertebra no. 7 (*right*). C, pterygiophores and dorsal fin rays. D, supraneurals and dorsal scutes. E, left pectoral girdle in lateral view.

neural arches. Each spine is high, acute, striated along its entire length and is slightly inclined backwards. The highest neural spines occur at about the middle of the dorsal fin, from where they start to shorten gradually, becoming more inclined backwards. Near the base of the caudal fin the spines become short, stout, and much more inclined.

The pleural ribs are very long and longitudinally furrowed. They are inclined backwards and arched forwards. They are carried by enlarged parapophyses, not fused to the centrum. Epineurals occur up to the centre of the dorsal fin. Epipleurals occur along the anterior half of the caudal region (text-figs. 1 and 3).

The haemal arches are relatively long, at least in the anterior part of the caudal region. The first caudal centrum bears only a haemapophysis. The haemal spines increase gradually in length, reaching a maximum in caudal vertebra 7, where the distal end of the haemal spine reaches the base of the anal fin. Hereafter backwards, the spines become shorter. Each of the first six haemal spines is flat and wide at its base, becoming sharp distally.

The caudal peduncle is short. The neural and haemal spines are flat, expanded, and sharp at their distal ends. They are strongly inclined backwards and fit tightly to each other. Three large oval scutes, with indented margins, are situated along the four terminal vertebrae, each overlapping the following scute, and together forming a lateral keel-like structure (text-fig. 7).

Three supraneurals are situated in front of the dorsal fin (text-fig. 5D). The first one is oval, with a wide supporting ridge along it. It supports the first dorsal scute from below. The second is high-triangular. It bears a longitudinal supporting ridge, expanding backwards and forwards at the distal end, and split at its proximal end, at about half its length. This element supports the second dorsal scute. The third supraneural is similar in form to the second, but does not support any scute.

Pectoral fin and girdle. The pectoral fin is ventral, carrying 14 unsegmented, distally branched fin rays. Its length is about that of 6·5 successive vertebrae, and almost twice the length of the pelvic fin. Complete pectoral girdles, including their dermal and endoskeletal elements, can be observed in specimens P.143 and P.163.

The cleithrum is flat and smooth supported all along its midline by a heavy, striated ridge. It is arched forward and terminates somewhat ventral to the posteroventral end of the preopercular. The bone becomes narrower towards its extremities.

The supracleithrum is thick and flat, rod-shaped, ornamented by longitudinal, closely spaced grooves. It touches the outer dorsal surface of the cleithrum, and is directed obliquely from posteroventral to anterodorsal. Its dorsal end is expanded posteriorly. The expansion is flat, rounded, and closely covered by tubercules. It is traversed by the lateral line canal on its way from the body to the head (text-fig. 5E).

The postcleithrum is exceptionally developed. It is thick, long, rod-like slightly arching in the posteroventral direction. The bone is longitudinally striated. Its proximal end is in contact with the posterior inner region of the supracleithrum. Ventrally it terminates at the horizontal level of the posteroventral corner of the mandible. The distal end is sharply bent posteriorly, almost reaching the anterior end of the pelvic girdle. The pair of postcleithra look like very large ribs, and most probably served as a support to the body wall of the very deep belly.

The dorsal arm of the posttemporal is well developed, wide, and triangular. The posterior corner of the triangle articulates with the supracleithrum. The apex of the triangle reaches the dorsal mid-line. The outer surface of the posttemporal is ornamented by prominent tuberculated ridges, scattered over the bone in a fan-like fashion, centred at the posterior corner of the triangle. The ventral arm of the posttemporal has the shape of a flattened rod with an enlarged base and is densely striated. It starts in front of the articulation point of the posttemporal with the supracleithrum. The lateral line canal traversed the posttemporal on its way from the supracleithrum to the head. The pores of the canal are distinct near to the articulation area.

The coracoid is a large thin trapezoidal plate, with a horizontal base extending slightly backwards. Its anterior margins are firmly jointed to the posteroventral margins of the cleithrum. A prominent

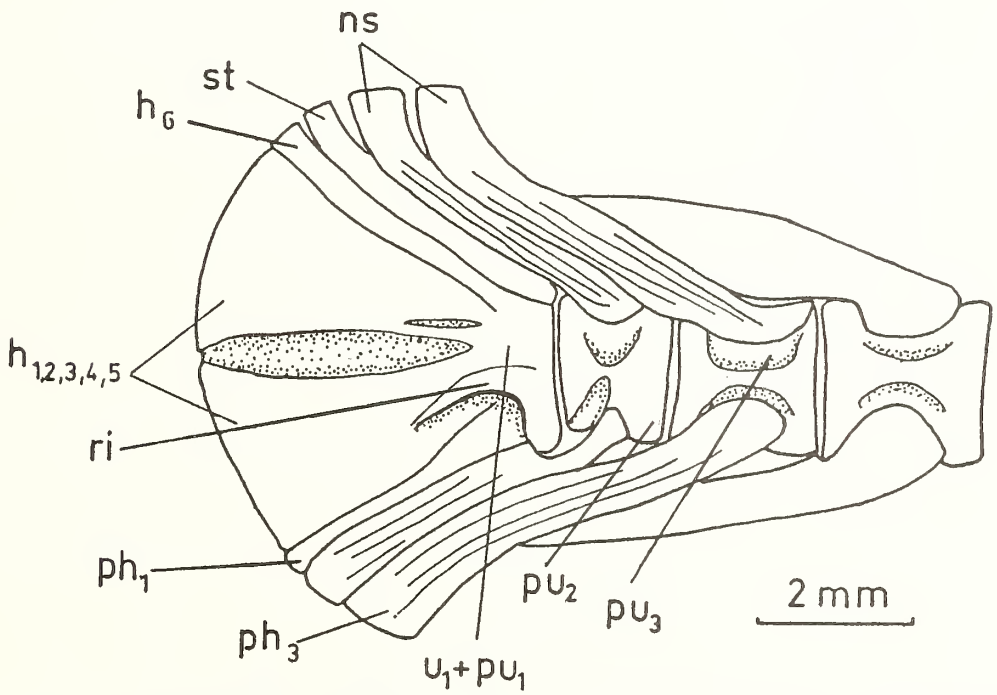
ridge extends from the centre of the coracoid to its anterior corner. The coracoid thickens near its contact with the scapula.

The scapula is small and thick relative to the coracoid, and has a large and distinct scapular foramen. Four radials can clearly be counted in the pectoral girdle (specimen P.163).

Pelvic fin and girdle. The pelvic fin is abdominal. It originates at the level of the sixth caudal vertebra. It consists of five to six unsegmented fin rays. These are longitudinally grooved and distally branched. The pelvic fin is half the length of the pectoral fin. The pelvic girdle is flat and thin, wedge-like, with a few longitudinal thickenings. Four radials exist.

Dorsal fin. The dorsal fin has a long base, and occupies most of the back. It is as long as nineteen successive vertebrae, and contains thirty fin rays. Its anterior part is high, shortening gradually posteriorly. Each lepidotrich is longitudinally grooved whereas the last two are completely bifurcated. The fin rays are unsegmented. The first pterygiophore is very expanded and forwardly inclined. The proximal segments of the pterygiophores are flat, truncated ventrally, with a longitudinal ridge. Their distal end is expanded in a nail-head form, with two articulation facets. The middle radial is wide and thick. The distal radial is also preserved as a small rounded element, embraced between the bases of the hemitrichia. The fin ray is attached anteriorly by its base to the distal radial of the preceding pterygiophore, and by its ventral side to the proximal radial of the underlying pterygiophore (text-fig. 5C). The head of each proximal radial is anteriorly in close contact with the middle element of the preceding pterygiophore, dorsal to the base of the fin ray and posterior to its middle radial. The middle and distal radials form together a continuous flexible support for the dorsal fin.

Anal fin. The anal fin extends along about eleven vertebrae on the posterior half of the venter. It starts opposite the mid-length of the dorsal fin and contains twenty-two blunt, longitudinally grooved, unsegmented fin rays. The lepidotrichia of the last several rays are split from their bases. The anterior



TEXT-FIG. 6. *Parenchodus longipterygius* n. g. et sp. Restoration of the endoskeleton of the caudal fin.

TEXT-FIG. 7. *Parenchodus longipterygius* n. g. et sp. P.1508, Upper Cenomanian, Kefar Shaul Formation, Jerusalem, Israel. Lateral view of the tail.

part of the anal fin is relatively high (as high as the length of four vertebrae), becoming lower posteriorly. The proximal elements of the pterygiophores have one or two longitudinal grooves and are truncated at their proximal end. The two anterior elements are thick and long, the following ones become gradually shorter. The distal elements of the pterygiophores are small, thin, with an undefined shape.

Caudal fin (text-figs. 6 and 7). The caudal fin is large, deeply forked. The dorsal lobe is somewhat longer than the ventral one. The dorsal and the ventral lobes contain ten and nine principal fin rays, respectively. These are segmented and branched distally. Nine segmented, undivided accessory fin rays precede the principal fin rays of each lobe.

The proximal ends of the principal fin rays, except for the two middle ones, are narrow and sharp. They embrace the hypural plate in such a way that their proximal ends almost meet. The two middle rays have a truncated, thickened base, only touching the posterior edge of the hypural plate, not embracing it.

The endoskeleton of the caudal fin consists of four vertebrae, namely, two separate preurals (pu_2, pu_3) and a ural vertebra fused to the first preural, to form a single triangular centrum. The hypurals are fused into one wide plate, which is divided by a relatively wide longitudinal furrow—the continuation of the vertebral axis—into a ventral and a dorsal part. An additional long and narrow

hypural occurs in close contact dorsally to the hypural plate. The terminal centrum ($u_1 + pu_1$) bears a high, narrow stegural. The neural and the haemal spines of pu_2 and pu_3 are thick, wide, their distal ends are truncated, and they are not fused to their centra. The surface of these elements is finely striated. The truncated distal margins of the haemal spines, the parhypurals, the hypurals, the stegural, and the neural spines of pu_2 and pu_3, form a continuous arched line constituting the posterior margin of a wide plate supporting the fin rays. A distinct semilunar ridge, arching ventrally, occurs on the ventrolateral area of the terminal centrum (text-fig. 7). Its ventral position as well as its direction hinders its identification as the uroneural of ural 1. It is probably only a thickening of the centrum of the vertebra, intended to enlarge the adhesion surface of the caudal fin muscles. A functionally similar element was recorded by Nursall (1963, p. 459). However, the two elements are not homologous, since Nursall's hypurapophysis is a lateral process of the anterior hypural whereas the element described here is a part of the terminal centrum. Summarizing the main features of the caudal skeleton, it is characterized by (1) fusion of the hypurals, (2) epaxial and hypaxial elements not fused to the centra—a primitive feature, (3) reduction in elements—epurals and uroneurals missing and, (4) the loss of ural 2.

Scales. The body is naked, without scales except for two dorsal scutes and a row of three lateral scutes at the base of the tail. The dorsal scutes are large, oval, not overlapping. They are situated along the dorsal mid-line, from the occiput to near the anterior end of the dorsal fin. The first scute is more than twice as large as the second. The scutes are supported by the two first supraneurals (text-fig. 5D).

The posterior part of each dorsal scute is ornamented by scattered tubercles whereas the anterior part bears tuberculated ridges, radiating from the centre of the scute. An inner supporting ridge runs along the posterior half of the scute.

Three relatively large scutes occur laterally along the four terminal vertebrae. They are thin, with indented margins, successively overlapping each other, to form a lateral keel-like structure (text-fig. 7).

DISCUSSION

The basic features of *Parenchodus* agree well with those used by Goody (1969) in defining the family Enchodontidae: Head and body high; posttemporal fossa unroofed; lower jaw long and posteriorly high; articular facet exposed laterally; opercular high, with convex posterior margins; preopercular without a ventral spine; pectoral fin ventral, larger than the pelvic fin; pelvic fin abdominal; existence of a few, non-overlapping dorsal scutes. Only one feature, namely the total reduction of the lateral line scales in *Parenchodus*, disagrees with Goody's diagnosis of the family. It seems that this feature is not enough for the erection of a separate family.

The tendency towards a short and deep body, indicated as one of the features defining the genus *Enchodus* (Goody 1976), and characterizing especially the old world species of *Enchodus*, is exhibited in extreme form in *Parenchodus*.

This tendency correlates well with other structural features, so typical of short and deep fish, namely: (1) reduction in number of vertebrae; (2) reduction in number of abdominal vertebrae (in *Parenchodus*, the abdominal vertebrae constitute only 25% of the total number of vertebrae); (3) shortening of the post- and preorbital regions; (4) enlargement of supraneurals, serving as a support to the high epaxial, post-cranial region; (5) long, rib-like postcleithra, supporting the belly; (6) long-based dorsal and anal fins, and a well-developed pectoral fin, providing manoeuvering ability. All of these features can be observed in other deep-body fishes such as *Pharmacichthys* and *Aipichthys* from the Cenomanian of Lebanon (Gayet 1980) or *Exellia* and *Ceratoichthys* from the Middle Eocene of Monte Bolca, Italy (Blot 1969).

Such a body-shape could be the result of a different habitat and mode of life of *Parenchodus* compared to the other genera of the family. *Enchodus* and *Palaeolycus* were active, mid-water, or pelagic predators (Goody 1969, 1976), whereas *Parenchodus* was a predator which probably lived among and in vertical reefal elements. Although the body of *Parenchodus* is not streamlined, the structure of the caudal fin indicates a good swimming ability. These features are as follows: (1) a well-developed and deeply forked caudal fin; (2) a stout peduncle; (3) a reduction in the elements of the

caudal skeleton as manifested by the fusion of the hypurals, and the lack of uroneurals and epurals; (4) a large contact area between the bases of the caudal fin rays and the hypurals; (5) a lateral expansion of the centre of the fused terminal vertebrae ($u_1 + pu_1$) enlarging the adhering area of the caudal fin muscles; (6) the lateral keel-like structure formed by the overlapping lateral scutes at the base of the tail (typical of fast-swimming fishes, Hildebrand 1976).

Parenchodus exhibits extremely the tendency of the family Enchodontidae towards a short body. This feature existed, though to a lesser degree, in the Old World *Enchodus*-species.

The short and high body of *Parenchodus* seems to be an adaptation to the special ecological conditions which prevailed in the sea in the area of Givat Shaul during the late Cenomanian.

Since no evidence for a reefal facies is exhibited in the Kefar Shaul Formation, the existence of such an environment should be looked for in the partly contemporaneous, rudist-containing Weradim Formation.

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ABBREVIATIONS USED IN TEXT-FIGURES

an	angular
cb	ceratobranchial
cl	cleithrum
co	coracoid
d	dentary
dpt	dorsal limb of the posttemporal
ec	ectopterygoid
en	endopterygoid
fds	first dorsal scute
fpn	first postneural
f	frontal
h_{1-6}	hypurals 1–6
ha	haemal arch
hm	hyomandibular
hs	haemal spine
ht	hemitrichium
ic	intercalar
io	infraorbital
le	lateral ethmoid
ll	lateral line canal
ls	lateral scute
me	mesethmoid
mn	foramen of the mandibular branch of the lateral line
mpt	metapterygoid
mt	largest mandibular tooth
mx	maxilla
na	neural arch
ns	neural spine
op	opercular
p	parietal
pa	palatine
pcl	postcleithrum
pf	pectoral fin
pfr	pectoral fin radial
ph	parhypural
pmx	premaxilla
pop	preopercular
ps	parasphenoid
pt	pterotic
ptf	posttemporal fossa
pu	preural
q	quadrate
r	pleural rib
ra	retroarticular
rd	distal radial
ri	ridge on the centrum $u_1 + pu_1$
rm	median radial
rp	proximal radial
rt	replacement tooth
sc	scapula
scf	scapular foramen
scl	supracleithrum
snf	spinal nerve foramen
so	supraoccipital
sop	subopercular
sp	sphenotic
ss	symphyseal suture of the mandibular
st	stegural
sy	symplectic
te	external teeth row
ti	internal teeth row
u	ural
vpt	ventral limb of the posttemporal